Object-form topology in the ventral temporal lobe

Response to I. Gauthier (2000)

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In her thoughtful comment on the functional organization of ventral temporal cortex, Isabel Gauthier clearly outlines the hypotheses that have been proposed and are currently being investigated with functional brain imaging [Gauthier, I. (2000) What constrains the organization of the ventral temporal cortex? *Trends Cognit. Sci.* 4, 1–2][1]. One of those models, which we call the object form topology hypothesis, was proposed by us in a recent paper[2] that motivated Gauthier's comment. In this reply, we would like to explain why we have proposed the object-form topology hypothesis and clarify what we believe are its most salient aspects.

As Gauthier correctly states, the results of the studies reported in Ishai *et al.*[2] can be accommodated by the category-specific module and process-map models and, therefore, should not by themselves compel one to abandon these proposals. We agree. The studies were not designed to test these models. In fact, they were originally designed to test whether the house-responsive region identified the region of cortex that processed all non-face objects. Nonetheless, for several reasons we felt compelled to propose the object-form topology hypothesis as an alternative to be considered.

First, our finding that chairs evoked a pattern of response distinct from that evoked by houses or faces led us to ponder the possibility that this proliferation of category-related patterns may not end with three categories. In fact, our research has indicated that other categories, namely animals, tools, and inverted faces, do indeed evoke distinct patterns of response in ventral temporal cortex[3–5]. In the case of tools, this distinct pattern includes the division of the house-responsive region in the medial fusiform gyrus into a lateral sector that responds maximally to houses and a medial sector that responds maximally to tools[3]. It seemed unlikely to us that the capacity of ventral temporal cortex to evince a unique pattern of activity for each category could be accommodated by a category-specific module hypothesis.

Second, our results also indicated that the representation of an object may not be restricted to the regions that respond maximally to that object. Distributed, overlapping representations of different object categories would have much greater capacity to produce unique patterns of response than would representations restricted to category-specific regions. Consequently, we thought that a model of the functional architecture of ventral temporal cortex that is based on widely distributed, overlapping representations would be more able to accommodate the proliferation of distinct, category-related patterns of response than would the other models.

Gauthier suggests that the results of the Ishai *et al.*[2] paper could be accommodated by the category-specific module and process-map models by positing the existence of three modules – spatial layout, faces, and non-face objects – or three processes – spatial processing, expert discrimination of visually-similar objects, and 'basic' level processing. As mentioned above, however, our other studies suggest that a three-way division will not be sufficient to accommodate results on category-related patterns of response. Let us take one of the three modules or processes, spatial layout processing in the parahippocampal place area (PPA), as an example.

It has become common to refer to the region that responds more to houses or buildings and the region that responds more to landscapes and interior spaces as the same region. In fact, they appear to be overlapping but not coextensive. Talairach brain atlas coordinates for these regions reveal that the center of the PPA is anterior to the center of the house-responsive region[2,5–7]. The house-responsive region appears to be more extensive and may include the PPA in its anterior aspect. Moreover, as mentioned above, within the medial fusiform region that responds more to houses than to faces, a medial sector responds more to tools than to houses whereas a lateral sector responds more to houses than to tools[3]. Instead of being a single region with a single function, therefore, the PPA/medial fusiform region has a heterogeneous functional architecture with at least three sectors that have been functionally distinguished thus far. Moreover, the general function of this entire region clearly is not well characterized as reflecting processing of the spatial layout of areas through which one can navigate because the region also responds strongly, and in some sectors maximally, to objects for which spatial layout is not a critical or dominant attribute, such as tools and chairs.

There are two aspects to the object-form topology hypothesis that we would like to keep distinct. The first, more critical aspect is the proposal that the functional architecture of ventral temporal cortex is a continuous representation of information about objects that has a topological arrangement. Our results demonstrate a remarkably consistent topological arrangement of regions showing category-related response preferences. Our results also demonstrate distinct category-related patterns of response that involve broad expanses of cortex suggesting that the topology is continuous and that representations for different types of objects are distributed and overlapping. The second aspect of the object-form topology hypothesis concerns the nature of the information about objects that is represented in ventral temporal cortex. We are the first to admit that the nature of this information and the principles that underlie its topological arrangement are unknown. We suggested that it may concern attributes of object-form because of its location in the ventral extrastriate visual cortex.

In her comment, Gauthier focuses on the second aspect of the object-form topology hypothesis, namely object-form attributes – which she renames 'visual features'. Gauthier seems to imply that under our hypothesis, the pattern of response in ventral temporal cortex would be passively driven by the visual features of a stimulus. We know, however, that the pattern of response in ventral temporal cortex is strongly modulated by attention. The pattern of response associated with an object category can be evoked when an example of that category and an example of another category are both present in the stimulus but selective attention is directed to only one object[8–10]. Category-related patterns of response can even be evoked by mental imagery[11,12] or by merely reading the names of objects[2], demonstrating that these patterns are not simply a function of the visual features of stimuli. Therefore, when Gauthier asks what the pattern of response would be to a chair that shares more visual features with a house than with a typical chair (p. 1), we would predict that if the stimulus is recognized as a chair, it would elicit a chair-related pattern of response. If an object is perceived as a chair, its dominant object-form attributes are those of a chair, even if it has more numerous house-like visual features. The nature of the object-form attributes that are represented in ventral temporal cortex, therefore, must be sufficiently abstract to support normal object recognition (seeing stimuli as objects, not as collections of visual features).

The most important aspect of the object-form topology hypothesis, however, is that the functional architecture of ventral temporal cortex consists of a continuous, topologically arranged representation of information about object-form in which the representations of different categories are distributed and overlapping. We would prefer, therefore, that the model not be termed the 'feature-map model' but prefer our own term, namely 'object-form topology'.

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The nature of the information about objects that is represented in ventral temporal cortex is a great puzzle. It may be attributes of object-form that are primitive and purely visual in nature, as suggested by Tanaka[13], or that are more abstract and perhaps integrated with the function or meaning of objects, as suggested here. It may be different types of processes that are performed to identify objects, as suggested by Gauthier. The information may be organized into areas with single functions or into a continuous, topologically-arranged map. The solution to this puzzle may tell us nothing less than the basis for our shared knowledge of object form. As clearly outlined by Gauthier, viable competing hypotheses exist for what form this solution may take. We wish to thank her for generating this opportunity to clarify and amplify our hypothesis. We look forward to a vigorous and productive period of investigation that we hope may lead to a neurobiological answer to an ancient question from epistemology.

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Monitor

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The hippocampus as an odour encoder

Despite decades of research, and a virtually consensual opinion among neuroscientists that the hippocampus is involved in some way in memory, the specific contribution of this region to cognition remains surprisingly elusive. This is perhaps partly because of the disparity between conclusions drawn from the human and animal literature. While clinical studies have focussed on the putative role of the hippocampus in memory for everyday, autobiographical episodes (which comprise many different types of information from a variety of modalities), animal research has emphasized the involvement of the hippocampus specifically in spatial memory, as studied in rodent learning paradigms such as the Morris swim task. Evidence that the rat hippocampus also processes *non*-spatial information might to help bridge the gap between the human and non-human literature, and would certainly provide information that would enrich our understanding of the putative functions of the hippocampus. A recent study by Wood *et al.* provides such evidence[1]. These authors recorded from neurones in the hippocampus during an odour-guided, delayed non-matching-to-sample task. One type of neuron responded when the rat was in a particular location – the well-known 'place cell' phenomenon that has provided such strong support for the spatial-memory hypothesis. In addition, however, neurones were observed that responded preferentially, not to a particular place, but to a particular odour. Hippocampal neurones therefore appear to encode, not only spatial 'map' information, but also information about individual items. This finding, combined with results from lesion experiments, suggests that the rat hippocampus is important for the memory of non-spatial as well as spatial information, a notion more in line with formulations of hippocampal function derived from the human literature. It can be hoped that further studies in humans and in other species will help in the search for the elusive functions of this important structure.

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Lexical memory

In order to remember a list of words, most people find it helpful to rehearse these words subvocally. Remembering words therefore clearly involves the retention of their phonological code. It is, however, still a matter of debate to what extent other information, such as lexical–semantic information, plays a role in memorizing verbal material, and at which point. Is lexical information required during retention or only when items need to be retrieved? Ruchkin *et al.* recently reported an ERP experiment that aimed to answer these questions[1]. Participants listened to a list of words and to a list of pronouncible nonwords, and were asked either to remember these items during a brief time period (memory task), or to remember whether the list had included two of the same items (detection task). The results showed that during the retention interval, the ERPs to the word condition showed a scalp distribution different from that in the non-word condition, but only in the memory task. This difference was already apparent during the presentation of the list of items, and it was shown that the difference was not due to a difference in memory load. There was no difference in the ERP distribution in the detection task These findings therefore support the view that lexical–semantic information contributes to the retention of words in working memory.

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